

Flexible Use of Patch-Leaving Mechanisms in a Parasitoid Wasp

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*Classical optimal-foraging theory predicts that a parasitoid is less likely to leave a patch after a host encounter when the host distribution is aggregated, whereas a parasitoid is more likely to leave after a host encounter when the host distribution is regular. Field data on host distributions in the area of origin of the whitefly parasitoid *Encarsia formosa* showed that whiteflies aggregate at several spatial scales. However, infested leaves most likely contained a single host. This suggests that a host encounter is not enough to decide when to leave. We therefore tested the effect of host distribution and parasitoid experience on patch-leaving behavior. Each parasitoid was observed for several consecutive days in a three-dimensional arena with leaflets containing on average one host per leaflet in an either regular or aggregated host distribution. A proportional hazards model showed that a host encounter decreased the leaving tendency on a leaflet with one host when the time since the latest host encounter was short, but increased the leaving tendency when the time since the latest host encounter was long, independent of host distribution. We conclude that a parasitoid can switch from decreasing to increasing its tendency*

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to leave a patch after a host encounter. We propose two hypotheses that may explain the evolution of such a switching mechanism.

KEY WORDS: optimal foraging; patch-leaving behavior; host distribution; *Encarsia formosa*; whitefly.

INTRODUCTION

Organisms evolve by natural selection to optimally use their limited time to find and exploit food and reproductive opportunities. Behavioral ecologists have developed a large body of optimal-foraging theory to understand the behavioral decisions that organisms make to achieve maximum lifetime reproductive success (Stephens and Krebs, 1986; Godfray, 1994; Houston and McNamara, 1999). Insect parasitoids have proven to be an ideal model system to test hypotheses generated by optimal-foraging theory. Patch use is an important aspect of their foraging process. Central to patch-use theory is the decision when to leave a patch and search for another. Many factors have been shown to affect patch-residence time, including contact with kairomones (Corbet, 1971), hosts (Waage, 1979; Driessen *et al.*, 1995) and other parasitoids (Visser *et al.*, 1992; Bernstein and Driessen, 1996; Wajnberg *et al.*, 2004); travel time (Wang and Keller, 2003); parasitoid experience (Papaj and Lewis, 1993); the state of the host (Outreman *et al.*, 2001); parasitoid genotype (Wajnberg *et al.*, 1999) and parasitoid species (Vos *et al.*, 1998; Wajnberg *et al.*, 2003); and the internal state of the parasitoid (Roitberg *et al.*, 1992; Outreman *et al.*, 2005).

Classical patch-leaving models like Charnov's (1976) marginal-value theorem assumed that the forager is omniscient. Limited experience was incorporated in simple rules of thumb, i.e. leave after a fixed time, after a fixed number of encounters or after a fixed giving up time (see Godfray, 1994). Iwasa *et al.* (1981) showed that the best rule depends on the distribution of prey (or hosts). Waage (1979) developed a more sophisticated patch-leaving rule where oviposition has an incremental effect on giving up time, leading to longer patch-residence times. Using statistical analysis of behavioral rules (e.g. Hemerik *et al.*, 1993), Driessen *et al.* (1995) proposed a count-down mechanism where oviposition has a decremental effect on giving up time, leading to shorter patch residence times. Host distribution is an important factor determining which mechanism is adaptive. Generally, an oviposition decreases the tendency to leave a patch when hosts are aggregated and increases the leaving tendency when hosts are regularly distributed. There is empirical evidence for both mechanisms (reviewed by van Alphen *et al.*, 2003).

To understand patch use and other foraging decisions by an insect parasitoid, it is indispensable to know the conditions under which this behavior has evolved. We have quantified natural host densities and distributions in the presumed area of origin of our model species, the whitefly parasitoid *Encarsia formosa* Gahan (Hymenoptera, Aphelinidae) (Burger *et al.*, 2004). *E. formosa* is famous for its successful use as biological control agent against whitefly (Homoptera: Aleyrodidae) (van Lenteren *et al.*, 1996; van Lenteren, 2000). Whitefly nymphs aggregated at several spatial scales in the field (Burger *et al.*, 2004), which suggests that *E. formosa* should decrease its tendency to leave after a host encounter. However, a leaflet with only one host was still the second most common type of leaflet after empty leaflets (Burger *et al.*, 2004). In such an environment, a single host encounter is not enough to decide whether to stay or to leave. The aggregated distribution suggests that there may be more hosts, but the drop in frequency of leaflets with more than one host suggests that most likely there are not. To study this dilemma, we quantified the leaving tendency of *E. formosa* during a large part of its life under experimental conditions that mimic those in the field.

Changing behavior with experience (learning) can be an adaptive mechanism when foraging cues are highly variable in a predictable way (Vet and Dicke, 1992; Papaj and Lewis, 1993; Vet *et al.*, 1995). In the field, the number of hosts on a leaflet was highly variable and the spatial dependence provides parasitoids with some degree of predictability on presence of hosts (Burger *et al.*, 2004). Greenhouse data showed that the whitefly distribution gradually changed from clustered towards regular in the course of time as a result of whitefly dispersal (Eggenkamp-Rotteveel Mansveld *et al.*, 1982). We therefore tested whether parasitoids learn to leave sooner when host distribution is regular than when host distribution is aggregated.

MATERIALS AND METHODS

Organisms

Tomato plants (Solanaceae, *Solanum lycopersicum* L. cv. Money-maker) were reared by Unifarm, Wageningen, the Netherlands, at 21°C, 70% R.H. and L:D = 16:8 h. Nymphs of the greenhouse whitefly *Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleyrodidae) were obtained from the whitefly rearing on tomato at the Laboratory of Entomology, Wageningen, the Netherlands (21°C, 70% R.H. and L:D = 16:8 h). Pupae of *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) parasitoids were

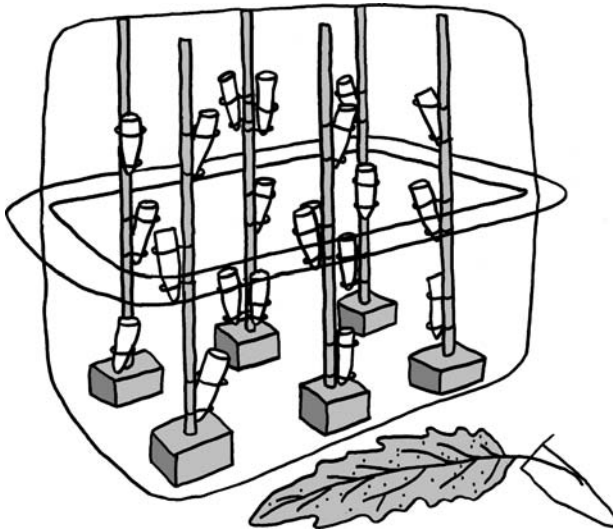


Fig. 1. Experimental arena ($l \times w \times h = 27 \times 18 \times 22$ cm). Each micro tube was filled with water, sealed with parafilm and holding one tomato leaflet (see foreground).

obtained from Koppert Biological Systems, Berkel en Rodenrijs, the Netherlands.

Experimental Arena

Preliminary experiments showed that a relatively large, 3-D setup was necessary to evoke natural leaf-hopping behavior. The experimental arena also had to be small enough to keep track of the parasitoids that are less than 1 mm in size. We designed the following arena to balance these opposing demands on the size of the experimental arena (Fig. 1).

The experimental arena was confined by two rectangular, colorless plastic containers (Multistar, Starplast, Tilburg, the Netherlands) encompassing an area of $27 \times 18 \times 22$ cm ($l \times w \times h$). In each container three holes (diameter 1.8 cm) were melted and covered by fine gauze for ventilation. Six wooden blocks ($3.2 \times 3.2 \times 1.8$ cm) were attached to the bottom of the arena in a 3×2 grid using double-sided adhesive tape, each block pierced to hold a vertical wooden stick (diameter 5 mm) mimicking a plant's branch. In total, 21 tomato leaflets were alternately attached to the sticks in three horizontal layers (a 3×2 grid has seven edges or inter-stick spaces). The

distance between sticks was about 9 cm and between layers about 6 cm. Each leaflet was put in a 1.5 ml micro tube that was filled with water and sealed with parafilm. Each micro tube was suspended in two rings of iron wire attached to one of the sticks. In this way, leaflets could be replaced and parasitoids were able to visit more than 21 leaflets present in the arena (see Observations section). Droplets of sucrose solution were provided on a piece of parafilm on the bottom of the arena to mimic presence of nectar.

Treatments

The effect of host distribution was studied using two treatments. In the treatment with a regular host distribution, each leaflet contained exactly one host on the lower side. This density corresponds to the average field density and the average density in the treatment with an aggregated host distribution. In the treatment with an aggregated host distribution, the number of nymphs on the lower side of a leaflet was drawn from a Poisson distribution with mean and variance equal to a spatially dependent λ based on field sampling of plants within spots along transects (Burger *et al.*, 2004). The average over 2500 leaflets was about 1.0 host per leaflet. Although the Poisson distribution is a random distribution, we showed that its mean was spatially dependent in the field (Burger *et al.*, 2004). The resulting frequency distribution is therefore much more skewed to the right (aggregated) than a Poisson distribution with the average λ (Fig. 2). Nymphs were carefully transferred from their original feeding site onto the leaflets. Previous experiments revealed that parasitoids still accept transferred nymphs for both oviposition and host feeding, and that *E. formosa* does not exploit herbivore-induced plant volatiles to locate hosts from a distance (Noldus and van Lenteren, 1990; Romeis and Zebitz, 1997; Sütterlin and van Lenteren, 2000). Only fourth nymphal stages were used because younger stages are easily damaged during transfer. The fourth stage is preferred for oviposition and is also fed upon in a no-choice situation (Nell *et al.*, 1976).

Observations

Parasitoids were kept and observed in a climate room at 30°C, about 60% RH and L:D = 12:12 h. On day 0, parasitoids were allowed to emerge during one to two hours in a Petri dish containing droplets of sucrose solution (10% w/w) on a piece of parafilm and kept herein until the next day. Preliminary observations revealed that parasitoids were basically inactive

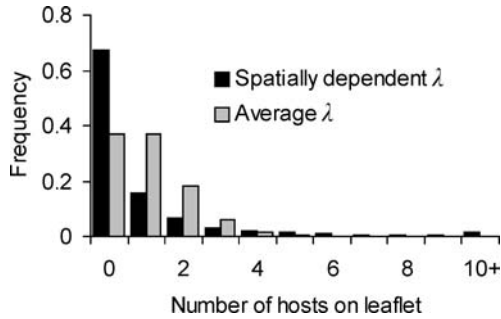


Fig. 2. Poisson distributions of number of hosts per leaflet. The first histogram (black bars; “Spatially dependent λ ”) was used in the treatment with an aggregated host distribution, based on field data on number of whitefly nymphs on leaflets collected from plants within spots along transects. The number of hosts per leaflet was drawn 2500 times from Poisson distributions with $\log(\lambda) = -1.422 + T_i + S_{j(i)} + P_{k(ij)}$, where T_i is the effect of the i th randomly selected transect and assumed independent $N(0, 0.522)$, $S_{j(i)}$ the effect of the j th spot randomly selected along the i th transect and assumed independent $N(0, 0.197)$, and $P_{k(ij)}$ the effect of the k th plant randomly selected within the j th spot along the i th transect and assumed independent $N(0, 2.485)$. $N(\mu, \sigma^2)$ is a normal distribution with mean μ and variance σ^2 . Parameters of this generalized linear mixed model were estimated from field data (Burger *et al.*, 2004). Thus, each number was drawn from a Poisson distribution with a different, spatially dependent, λ . The second histogram (gray bars; “Average λ ”) shows the Poisson distribution with λ equal to the average of all spatially dependent λ 's. This illustrates that a Poisson distribution with a spatially dependent λ can result in an aggregated host distribution.

during the day of emergence. On day one, one parasitoid per arena was introduced on a leaflet between 8:00 and 9:00. Two parasitoids, one at the regular host distribution and one at the aggregated host distribution, were observed simultaneously by one observer taking turns with another observer. The following behaviors were recorded continuously in time (min): landing on leaflet, changing leaflet side, contacting host, inserting ovipositor, host feeding, honeydew feeding, leaving host, leaving leaflet, sucrose feeding, leaving sucrose source. Once a leaflet was visited, it was replaced when the parasitoid landed on another leaflet, actively fed from the sucrose solution or spent 15 min away from the leaflet. This procedure mimics parasitoids

foraging in spatially endless vegetation. The drawback is that parasitoids cannot return to favorable patches but have to search for new ones instead. Parasitoids were removed 10 h after introduction into the arena and kept in a Petri dish with sucrose solution until the next day. The next day, all nymphs were replaced in the latest configuration by newly-transferred nymphs from the rearing (see subsection Materials). To incorporate patch depletion, parasitoids were introduced on the same leaflet from which they were taken the day before, with the number of nymphs on that leaflet decreased by the number encountered on that leaflet the previous day. Each parasitoid was observed individually from day one until it died, escaped or reached the end of day 6 ($N=5$ parasitoids per treatment). In the presence of hosts and honey/ honeydew, mean life span of *E. formosa* is about 4 days at 30°C (van Roermund and van Lenteren, 1992).

Statistical Analysis

Times to patch-leaving events were analyzed using a proportional hazards model (Cox, 1972; Kalbfleish and Prentice, 1980; Haccou and Hemerik, 1985). It models the multiplicative effects of p time-independent predictor variables X_i ($i=1, \dots, p$) on the hazard rate $h(t, X_1, \dots, X_p)$, which is the tendency (a probability per unit time) to leave a patch at time t :

$$h(t, X_1, \dots, X_p) = h_0(t) \exp \left(\sum_{i=1}^p b_i X_i \right), \quad (1)$$

where $h_0(t)$ is the baseline leaving tendency when all predictor variables are 0, and b_i is the parameter that shows the direction and relative strength of the effect of the i th predictor variable. The baseline tendency to leave a patch (the baseline hazard) is reset after landing on a leaflet or after handling a host (these are renewal points). Table I summarizes in which cases the time from a renewal point until the event was censored, and which predictor variables were tested. We analyzed the leaving tendency only on leaflets with one host to test the effect of experience rather than host density.

Partial deviance tests were used to decide which combination of main effects and one-level interactions was the most parsimonious (Neter *et al.*, 1996). Interactions were only considered with the accessory main effects included. When p time-independent predictor variables X_1-X_p (Table I) are selected in the most parsimonious model, 95% confidence limits for given values of X_1, \dots, X_p , denoted by column vector $X_h = (X_{h,1}, \dots, X_{h,p})^T$, are

Table I. Definitions of Censored Observations and Tested Predictor Variables of a Proportional Hazards Model for the Tendency to Leave a Leaflet with One Host

Event	
Leaving ^{a, b}	
Censored observations	
Leaving unintentionally ^b	
Host encounter	
Parasitoid out of sight	
Predictor variables	
Host distribution ^c	n.s.
Time since start of observation (days) ^d	X_1
Time since latest host encounter (min) ^e	X_2
Host encountered since landing on current leaflet (no/yes) = (0/1)	X_3

^aTimes only used when time since latest host encounter was non-missing. Leaving tendency was only considered on leaflets with one host to test the effect of experience rather than host density.

^bIntentionally: without interference by the observer. Unintentionally: disturbed or removed after 10 h of observation.

^cHost distribution was either regular or aggregated.

^dTime was measured in minutes and divided by 1440 min per day.

^eTime since latest host encounter was tracked globally, i.e. the latest host encounter was not necessarily on the current leaflet.

given by:

$$h(t, X_{h,1}, \dots, X_{h,p}) = h_0(t) \exp \left(\left(\sum_{i=1}^p b_i X_{h,i} \right) \pm t \left(\frac{\alpha}{2}; n-p \right) \sqrt{X_h^T \Sigma_b X_h} \right), \quad (2)$$

where Σ_b is the variance-covariance matrix of vector b consisting of the estimated regression coefficients b_1 – b_p . The critical value of the Student's t distribution $t(\alpha/2; n-p)$ was approximated by 2.

RESULTS

The most parsimonious proportional hazards model on the tendency to leave a leaflet with one host was $h(t, X_1, X_2, X_3) = h_0(t) \exp(0.062 X_1 - 0.065 X_2 - 0.475 X_3 + 0.049 X_2 X_3)$, where X_1 is time since start of observation (days), X_2 is time since latest host encounter (min) and X_3 is host encountered since landing on the current leaflet (no/yes) = (0/1) ($\chi_1^2 = 6.76$, $P = 0.009$) (Table I). Incorporation of host distribution thus did not significantly improve the model. The cumulative tendency to leave increased more or less linearly with time. Therefore, the baseline hazard $h_0(t)$ was estimated

by dividing the number of events by the sum of censored times and times until the event, i.e. 714/11964 per min. Dividing $\ln(2)$ by the baseline hazard (van Roermund *et al.*, 1994) results in a median residence time of 12 min on a leaflet with one host. Parasitoids encountered on average (\pm SE) 10.4 ± 1.3 (regular distribution) and 10.7 ± 2.4 (aggregated distribution) hosts per day.

Figure 3 shows $h(t, X_1, X_2, X_3)$, the tendency to leave a leaflet with one host (per min), before and after the host was encountered in relation to time since latest host encounter (min) and time since start of observation (days). The tendency to leave decreased with time since latest host encounter ($b_2 = -0.065$ per min). Parasitoids that did not encounter the host ($X_3 = 0$) had a *higher* tendency to leave than parasitoids that already encountered the host ($X_3 = 1$) when the time since latest host encounter (X_2) was *less* than 10 min (X_2 where hazard rates for $X_3 = 0$ and $X_3 = 1$ intersect, i.e. b_3/b_4). When the time since latest host encounter was *more* than 10 min, parasitoids that did not encounter the host had a *lower* tendency to leave than parasitoids that already encountered the host.

Alternatively, suppose a parasitoid enters a leaflet with one host. Its leaving tendency is then $h(t, X_1, X_2, 0)$, which can be anywhere along the dashed line (Fig. 3). As time progresses, so does time since latest host encounter X_2 . When the parasitoid encounters the host, its leaving tendency becomes $h(t, X_1, 0, 1)$, which is at the start of the solid line. Whether this is an increase or decrease in leaving tendency depends on the time since latest host encounter. If time since latest host encounter was longer than 7 min (X_2 where $h(t, X_1, X_2, 0) = h(t, X_1, 0, 1)$, i.e. b_3/b_2), the host encounter increased the leaving tendency. If time since latest host encounter was shorter than 7 min, the host encounter decreased the leaving tendency. The latter is more likely when the leaflet contains more than one host. In other words, the parasitoid switches from decreasing to increasing its tendency to leave after a host encounter as the time since latest host encounter lapses. Over time, the leaving tendency increased ($b_1 = 0.062$ per day), but the switching mechanism remained.

DISCUSSION

Our analysis of patch-leaving behavior over the course of a parasitoid's lifetime suggests that *E. formosa* switches from decreasing to increasing the tendency to leave after a host encounter as the time since latest host encounter lapses. The leaving tendency on a leaflet with one host decreased after host encounter when time since latest host encounter was short, but increased after host encounter when time since latest host encounter was

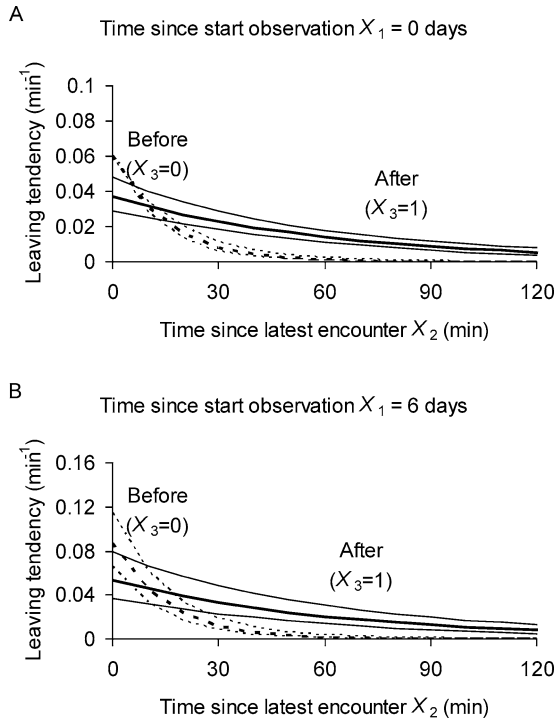


Fig. 3. Leaving tendency (per min) including 95% confidence limits on leaflets with one host in relation to time since latest host encounter (min), before (*dashed lines*) and after (*solid lines*) the host was encountered since landing on the leaflet. Time since start of observation was (a) 0 days and (b) 6 days. Most parsimonious proportional hazards model: $h(t, X_1, X_2, X_3) = 714/11964 \exp(0.062 X_1 - 0.065 X_2 - 0.475 X_3 + 0.049 X_2 X_3)$, where X_1 is time since start of observation (days), X_2 is time since latest host encounter (min) and X_3 is host encounter since landing on current leaflet (no/yes) = (0/1). Host distribution was included in the analysis but not significant. Host encounter decreased the leaving tendency when time since latest host encounter was short, but increased the leaving tendency when time since latest host encounter was long.

long, independent of host distribution. Thus, the patch-leaving mechanism is conditional upon the time since latest host encounter.

A switching mechanism was hypothesized previously by Driessen and Bernstein (1999). Their study was motivated by the fact that both increased and decreased leaving tendencies were reported after host encounter for the parasitoid *Venturia canescens*. Driessen and Bernstein (1999) argued

that a parasitoid can better distinguish between kairomone concentrations at low host densities than at high host densities. As host density increases, the reliability of information decreases, and parasitoids were expected to switch from an increased to a decreased leaving tendency after host encounter. In contrast, their results showed that *V. canescens* increased its leaving tendency after host encounter irrespective of kairomone concentration. Using a modeling approach, they showed that this mechanism produces the highest reproductive rate under field conditions. However, they did not model a switching mechanism as an alternative strategy.

One experimental study did show a switching patch-leaving mechanism (Outreman *et al.*, 2005). This switch was not driven by host density as expected by Driessen and Bernstein (1999), but by egg depletion. The parasitoid (*Aphidius rhopalosiphi*) initially decreased its leaving tendency after oviposition because its aphid host has an aggregated distribution. But the parasitoid gradually switched to increasing its leaving tendency after oviposition as the total number of previous ovipositions increased. These results are consistent with optimal-foraging models that predict that parasitoids should become more selective and more reluctant to superparasitize as they approach their expected lifetime reproductive success (Clark and Mangel, 2000). However, egg depletion is a more reliable indicator of the expected lifetime reproductive success for parasitoids with a high ovigeny index such as *A. rhopalosiphi* (Jervis *et al.*, 2001) than for parasitoids with a low ovigeny index such as *E. formosa*.

We propose two more fundamental hypotheses for the adaptive evolution of a switching mechanism. These hypotheses are not meant to be mutually exclusive or exhaustive. It is well established that parasitoids and predators use herbivore-induced plant volatiles to locate their herbivorous hosts or prey (Vet and Dicke, 1992; Steidle and van Loon, 2003). However, several studies showed that *E. formosa* does not (Noldus and van Lenteren, 1990; Sütterlin and van Lenteren, 2000; Romeis and Zebitz, 1997; van Roermund and van Lenteren, 1995; van Lenteren *et al.*, 1976; but see Birkett *et al.*, 2003). Rodriguez-Saona *et al.* (2003) found that plants infested by the silverleaf whitefly emitted plant volatiles similar to undamaged plants. They also found that plants infested with beet armyworm and whitefly emitted less volatiles than plants infested with only beet armyworm. Perhaps the feeding behavior of whiteflies, and in general of phloem feeders with intercellular stylet penetration (Turlings *et al.*, 1998), suppresses volatile emission. Whatever the reason may be, these studies suggest that *E. formosa* cannot estimate patch quality based on kairomone concentration. This is a fundamental difference with most patch-leaving models, which assume that the initial responsiveness or leaving tendency is based on kairomone concentration. The absence of or the parasitoid's

inability to exploit herbivore-induced volatiles implies that *E. formosa* can only rely on its experience within and between patches to assess the quality of its environment. This may have led to the evolution of a more flexible use of patch-leaving mechanisms.

The other potential explanation for the adaptive evolution of a switching mechanism is spatial or temporal variation in host distribution. The switching mechanism that we found allows a randomly searching parasitoid to exploit highly infested patches but also prevents them from wasting time in more common poor patches. Using time since latest host encounter may also enable the parasitoid to deal with temporal variation in host availability, i.e. to forage efficiently at different host distributions. Although sample sizes were low, this could explain why host distribution was not significant contrary to our hypothesis and why mean host-encounter rates were similar in both treatments. Vos *et al.* (1998) found that *Cotesia glomerata* parasitoids used a different patch-exploitation rule when foraging for a gregarious host species than when foraging for a solitary host species. Foraging at different host distributions may be natural for *E. formosa*, because whitefly distributions can change over time, at least in the greenhouse (Eggenkamp-Rotteveel Mansveld *et al.*, 1982).

In addition to these two ultimate explanations, we briefly discuss the proximate causes. Learning is a mechanism that enables a parasitoid to adaptively respond to a fluctuating environment. Infochemicals are generally considered a major source of information (Vet, 1999). Our model suggests that in the absence of detectable infochemicals time since latest host encounter is an important source of information for the parasitoid to learn about its environment. Time since latest host encounter could be stored in the parasitoid's memory or may be correlated with its physiological state. Long-term memory (hours to days) has been shown in *Drosophila* (Yin *et al.*, 1994), the honeybee (Menzel and Muller, 1996) and at least two parasitoid species (Takasu and Lewis, 1996; Kaiser *et al.*, 2003). An organism's physiological state is a major predictor of foraging behavior (Clark and Mangel, 2000; Houston and McNamara, 1999). Outreman *et al.* (2005) recently showed that the effect of an oviposition on the tendency to leave depended on the parasitoid's egg load.

Switching between patch-leaving mechanisms may be more common than reported (reviewed by van Alphen *et al.*, 2003). Van Roermund *et al.* (1994) found that the leaving tendency of *E. formosa* decreased significantly after one or more ovipositions in unparasitized hosts. In contrast to our experiment, however, they only observed intra-patch behavior on a single leaflet and therefore could not consider inter-patch experience. Between-patch experience is also ignored in the models by Waage (1979) and Driessen *et al.* (1995). Tenhumberg *et al.* (2001) showed

theoretically that optimal-foraging behavior is affected by the scale of aggregation.

We hope our results will stimulate theoretical studies that compare the incremental, decremental and switching patch-leaving mechanism for parasitoids that can and cannot use kairomones, under constant and fluctuating host distributions. This could test the hypotheses that lack of kairomone use or seasonal changes in host distribution drive the evolution of a switching mechanism. We can only speculate about the reasons for why the leaving tendency decreases with time since latest host encounter ($b_2 < 0$). One possible explanation is that parasitoids that enter the leaflet with a long time since latest host encounter are more likely to forage in the treatment with the aggregated host distribution. Our results should stimulate more long-term experiments focusing on inter-patch experience at larger spatial scales.

In conclusion, *E. formosa* switches from decreasing to increasing the tendency to leave after a host encounter as the time since latest host encounter lapses. We suggest this could be an efficient strategy for a parasitoid that searches randomly between poor patches but occasionally (in space or time) encounters a rich patch.

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REFERENCES

- Bernstein, C., and Driessen, G. (1996). Patch-marking and optimal search patterns in the parasitoid *Venturia canescens*. *J. Anim. Ecol.* **65**: 211–219.
- Birkett, M. A., Chamberlain, K., Guerrieri, E., Pickett, J. A., Wadhams, L. J., and Yasuda, T. (2003). Volatiles from whitefly-infested plants elicit a host-locating response in the parasitoid, *Encarsia formosa*. *J. Chem. Ecol.* **29**: 1589–1600.
- Burger, J. M. S., Gort, G., van Lenteren, J. C., and Vet, L. E. M. (2004). Natural history of whitefly in Costa Rica: An evolutionary starting point. *Ecol. Entomol.* **29**: 150–163.
- Charnov, E. L. (1976). Optimal foraging, marginal value theorem. *Theor. Pop. Biol.* **9**: 129–136.
- Clark, C. W., and Mangel, M. (2000). *Dynamic State Variable Models in Ecology*, Oxford University Press, Oxford.
- Corbet, S. A. (1971). Mandibular gland secretion of larvae of flour moth, *Anagasta kuehniella*, contains an epideictic pheromone and elicits oviposition movements in a hymenopteran parasite. *Nature* **232**: 481–484.
- Cox, D. R. (1972). Regression models and life tables. *J. R. Statist. Soc. B* **34**: 187–220.
- Driessen, G., and Bernstein, C. (1999). Patch departure mechanisms and optimal host exploitation in an insect parasitoid. *J. Anim. Ecol.* **68**: 445–459.
- Driessen, G., Bernstein, C., van Alphen, J. J. M., and Kacelnik, A. (1995). A count-down mechanism for host search in the parasitoid *Venturia canescens*. *J. Anim. Ecol.* **64**: 117–125.

- Edgenkamp-Rotteveel Mansveld, M. H., van Lenteren, J. C., Ellenbroek, J. M., and Woets, J. (1982). The parasite-host relationship between *Encarsia formosa* (Hym., Aphelinidae) and *Trialeurodes vaporariorum* (Hom., Aleyrodidae). XII. Population dynamics of parasite and host in a large, commercial glasshouse and test of the parasite-introduction method used in the Netherlands. *Z. angew. Entomol.* **93**: 113–130 (first part); 258–279 (second part).
- Godfray, H. C. J. (1994). *Parasitoids: Behavioral and Evolutionary Ecology*, Princeton University Press, Princeton.
- Haccou, P., and Hemerik, L. (1985). The influence of larval dispersal in the cinnabar moth (*Tyria jacobaeae*) on predation by the red wood ant (*Formica polyctena*): An analysis based on the proportional hazards model. *J. Anim. Ecol.* **54**: 755–770.
- Hemerik, L., Driessen, G., and Haccou, P. (1993). Effects of intra-patch experiences on patch time, search time and searching efficiency of the parasitoid *Leptopilina clavipes*. *J. Anim. Ecol.* **62**: 33–44.
- Houston, A. I., and McNamara, J. M. (1999). *Models of Adaptive Behaviour*, Cambridge University Press, Cambridge.
- Iwasa, Y., Higashi, M., and Yamamura, N. (1981). Prey distribution as a factor determining the choice of optimal foraging strategy. *Am. Nat.* **117**: 710–723.
- Jervis, M. A., Heimpel, G. E., Ferns, P. N., Harvey, J. A., and Kidd, N. A. C. (2001). Life-history strategies in parasitoid wasps: A comparative analysis of 'ovigeny'. *J. Anim. Ecol.* **70**: 442–458.
- Kaiser, L., Perez-Maluf, R., Sandoz, J. C., Pham-Delegue, M. H. (2003). Dynamics of odour learning in *Leptopilina boulandi*, a hymenopterous parasitoid. *Anim. Behav.* **66**: 1077–1084.
- Kalbfleisch, J. D., and Prentice, R. L. (1980). *The Statistical Analysis of Failure Time Data*, Wiley, New York.
- van Lenteren, J. C. (2000). A greenhouse without pesticides: Fact or fantasy? *Crop Protection* **19**: 375–384.
- van Lenteren, J. C., Nell, H. W., Sevenster-van der Lelie, L. A., and Woets, J. (1976). The parasite-host relationship between *Encarsia formosa* (Hymenoptera: Aphelinidae) and *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae). I. Host finding by the parasite. *Entomol. Exp. Appl.* **20**: 123–130.
- van Lenteren, J. C., van Roermund, H. J. W., and Sütterlin, S. (1996). Biological control of greenhouse whitefly (*Trialeurodes vaporariorum*) with the parasitoid *Encarsia formosa*: How does it work? *Biol. Control* **6**: 1–10.
- Menzel, R., and Muller, U. (1996). Learning and memory in honeybees: From behavior to neural substrates. *Annu. Rev. Neurosci.* **19**: 379–404.
- Nell, H. W., Sevenster-van der Lelie, L. A., Woets, J., and van Lenteren, J. C. (1976). The parasite-host relationship between *Encarsia formosa* (Hymenoptera: Aphelinidae) and *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae). II. Selection of host stages for oviposition and feeding by the parasite. *Z. angew. Entomol.* **81**: 372–376.
- Neter, J., Kutner, M. H., Nachtsheim, C. J., and Wasserman, W. (1996). *Applied Linear Statistical Models*, 4th ed., WCB/McGraw-Hill, Boston.
- Noldus, L. P. J. J., and van Lenteren, J. C. (1990). Host aggregation and parasitoid behaviour: Biological control in a closed system. In Mackauer, M., Ehler, L. E., and Roland, J. (Eds.), *Critical Issues in Biological Control*, Intercept, Andover, pp. 229–262.
- Outreman, Y., Le Ralec, A., Wajnberg, E., and Pierre, J. S. (2001). Can imperfect host discrimination explain partial patch exploitation in parasitoids? *Ecol. Entomol.* **26**: 271–280.
- Outreman, Y., Le Ralec, A., Wajnberg, E., and Pierre, J. S. (2005). Effects of within- and among-patch experiences on the patch-leaving decision rules in an insect parasitoid. *Behav. Ecol. Sociobiol.* **58**: 208–217.
- Papaj, D. R., and Lewis, A. C. (1993). *Insect Learning: Ecological and Evolutionary Perspectives*, Chapman and Hall, London.
- Rodriguez-Saona, C., Crafts-Brandner, S. J., and Canas, L. A. (2003). Volatile emissions triggered by multiple herbivore damage: Beet armyworm and whitefly feeding on cotton plants. *J. Chem. Ecol.* **29**: 2539–2550.

- Roitberg, B. D., Mangel, M., Lalonde, R. G., Roitberg, C. A., van Alphen, J. J. M., and Vet, L. (1992). Seasonal dynamic shifts in patch exploitation by parasitic wasps. *Behav. Ecol.* **3**: 156–165.
- Romeis, J., and Zebitz, C. P. W. (1997). Searching behaviour of *Encarsia formosa* as mediated by colour and honeydew. *Entomol. Exp. Appl.* **82**: 299–309.
- Steidle, J. L. M., and van Loon, J. J. A. (2003). Dietary specialization and infochemical use in carnivorous arthropods: testing a concept. *Entomol. Exp. Appl.* **108**: 133–148.
- Stephens, D. W., and Krebs, J. R. (1986). *Foraging Theory*, Princeton University Press, Princeton.
- Sütterlin, S., and van Lenteren, J. C. (2000). Pre- and post-landing response of the parasitoid *Encarsia formosa* to whitefly hosts on *Gerbera jamesonii*. *Entomol. Exp. Appl.* **96**: 299–307.
- Takasu, K., and Lewis, W. J. (1996). The role of learning in adult food location by the larval parasitoid, *Microplitis croceipes* (Hymenoptera: Braconidae). *J. Insect Behav.* **9**: 265–281.
- Tenhuberg, B., Keller, M. A., Tyre, A. J., and Possingham, H. P. (2001). The effect of resource aggregation at different scales: optimal foraging behavior of *Cotesia rubecula*. *Am. Nat.* **158**: 505–518.
- Turlings, T. C. J., Bernasconi, M., Bertossa, R., Bigler, F., Caloz, G., and Dorn, S. (1998). The induction of volatile emissions in maize by three herbivore species with different feeding habits: Possible consequences for their natural enemies. *Biol. Control* **11**: 122–129.
- van Alphen, J. J. M., Bernstein, C., and Driessen, G. (2003). Information acquisition and time allocation in insect parasitoids. *TREE* **18**: 81–87.
- van Roermund, H. J. W., and van Lenteren, J. C. (1992). The parasite-host relationship between *Encarsia formosa* (Hymenoptera: Aphelinidae) and *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae). XXXV. Life-history parameters of the greenhouse whitefly parasitoid *Encarsia formosa* as a function of host stage and temperature. *Wageningen Agric. Univ. Papers* **92.3**: 103–147.
- van Roermund, H. J. W., and van Lenteren, J. C. (1995). Residence times of the whitefly parasitoid *Encarsia formosa* on tomato leaflets. *J. Appl. Entomol.* **119**: 465–471.
- van Roermund, H. J. W., Hemerik, L., and van Lenteren, J. C. (1994). Influence of intra-patch experiences and temperature on the time allocation of the whitefly parasitoid *Encarsia formosa*. *J. Insect Behav.* **7**: 483–501.
- Vet, L. E. M., and Dicke, M. (1992). Ecology of infochemical use by natural enemies in a tritrophic context. *Annu. Rev. Entomol.* **37**: 141–172.
- Vet, L. E. M., Lewis, W. J., and Cardé, R. T. (1995). Parasitoid foraging and learning. In Bell, W., and Cardé, R. T. (Eds.), *Chemical Ecology in Insects*, 2nd ed., Chapman and Hall, London, pp. 65–101.
- Vet, L. E. M. (1999). From chemical to population ecology: Infochemical use in an evolutionary context. *J. Chem. Ecol.* **25**: 31–49.
- Visser, M. E., van Alphen, J. J. M., and Hemerik, L. (1992). Adaptive superparasitism and patch time allocation in solitary parasitoids—an ESS model. *J. Anim. Ecol.* **61**: 93–101.
- Vos, M., Hemerik, L., and Vet, L. E. M. (1998). Patch exploitation by the parasitoids *Cotesia rubecula* and *Cotesia glomerata* in multi-patch environments with different host distributions. *J. Anim. Ecol.* **67**: 774–783.
- Waage, J. K. (1979). Foraging for patchily-distributed hosts by the parasitoid, *Nemeritis canescens*. *J. Anim. Ecol.* **48**: 353–371.
- Wajnberg, E., Curty, C., and Colazza, S. (2004). Genetic variation in the mechanisms of direct mutual interference in a parasitic wasp: Consequences in terms of patch-time allocation. *J. Anim. Ecol.* **73**: 1179–1189.
- Wajnberg, E., Gonsard, P. A., Tabone, E., Curty, C., Lezcano, N., and Colazza, S. (2003). A comparative analysis of patch-leaving decision rules in a parasitoid family. *J. Anim. Ecol.* **72**: 618–626.
- Wajnberg, E., Rosi, M. C., and Colazza, S. (1999). Genetic variation in patch time allocation in a parasitic wasp. *J. Anim. Ecol.* **68**: 121–133.

- Wang, X. G., and Keller, M. A. (2003). Patch time allocation by the parasitoid *Diadegma semiclausum* (Hymenoptera: Ichneumonidae). I. Effect of interpatch distance. *J. Insect Behav.* **16**: 279–293.
- Yin, J. C. P., Wallach, J. S., Del Vecchio, M., Wilder, E. L., Zhou, H., Quinn, W. G., and Tully, T. (1994). Induction of a dominant negative CREB transgene specifically blocks long-term memory in *Drosophila*. *Cell* **79**: 49–58.